BRENESIA 21: 47-66. 1983

AN INTRODUCTION TO THE FRESHWATER FISH COMMUNITIES OF CORCOVADO NATIONAL PARK, COSTA RICA

Kirk O. Winemiller

Department of Zoology, University of Texas, Austin, Texas, USA 78712

Key Word Index: Corcovado, Costa Rica, fish communities, freshwater ecosystems, trophic relationships

ABSTRACT

The distributional pattern and ecology of each species of the freshwater fish communities surrounding the Sirena station of Corcovado Park were investigated during the early rainy season of 1982. Thirty species were observed or collected in freshwaters of the park, and an additional 10 species were restricted to intertidal regions. Peripheral division and invading marine fishes were major integral components of the freshwater ichthyofauna. These forms were particularly prevalent in the rivers and lower stretches of small streams. Stream width was positively correlated with species richness. Most of the primary and secondary division fishes appeared to be fairly restricted in their use of the range of available food resources. The habitat affinities and approximate abundances of each fish species was reported, based on visual censuses. The route of dispersal into the region by primary and secondary division fishes is discussed. Based on comparisons with earlier studies in Costa Rica and Panama, it is hypothesized that the marine elements in the park's freshwater ecosystems decline during the dry seasons. Food webs for the Quebrada Camaronal and Río Claro fish communities were constructed. The major sources of primary productivity for the communities are apparently allochthonous, indicating a dependency of the present ichthyofauna on the tropical rainforest as a source of energy and nutrients.

The freshwater ecosystems of Corcovado National Park in Costa Rica are unusual in permitting the study of freshwater tropical fish communities in a region of relatively low freshwater fish species diversity. Freshwater fish communities in the neotropics are generally characterized by an abundance of primary freshwater fish species (i.e. members of families with little or no tolerance to saline conditions) of the suborders Characoidei and Siluroidei (Lowe-McConnell, 1975). By marked contrast, the freshwater fish fauna of Corcovado contains only three species of primary freshwater fishes (two characoids and one siluroid), and this has been attributed to geographical factors inhibiting invasion by these forms onto the Osa Peninsula (Constantz *et al.*, 1981). Secondary division freshwater species (i.e., members of families with limited degrees of tolerance to marine salinities) are underrepresented at Corcovado as well, with only three reported (Constantz *et al.*, 1981) from the more than 25 secondary division species known from the Costa Rican mainland (Bussing, 1967). The remainder of the Corcovado freshwater fish fauna is comprised of peripheral division and marine species which have invaded the streams, often many kilometers inland. I have chosen to define peripheral division species as members of families which are clearly marine in origin, yet they must reside in fresh or brackish coastal waters for variable periods of time during their life histories. Peripheral fishes may require freshwater ecosystems for successful feeding during juvenile or adult life, or as an environment for reproduction and/or larval feeding. Marine fishes will be defined as species which may reside in fresh or brackish waters, often for extensive periods, yet they are fully capable of completing their entire life cycles in the marine environment. Unlike peripheral division fishes, many populations of marine fishes reside exclusively in the marine environment, either offshore or in intertidal zones. The significance of this new distinction will become apparent in subsequent sections of this report.

Constantz *et al.* (1981) reported a total of 20 fishes from the freshwaters of Corcovado Park. This represents relatively low species richness for neotropical freshwaters in a region of this size. The freshwater ecosystems of Corcovado Park provide good opportunities for comparatively-based hypotheses concerning freshwater fish dispersal abilities, historical aspects shaping local species diversity, and tropical freshwater community dynamics. The present study was undertaken to: 1) provide more detailed information on the relative abundances, distributions, and habitat utilization of each freshwater fish species; 2) determine the food habits of each fish species; 3) obtain information on the trophic structure of the freshwater ecosystems; and 4) provide a preliminary record of intertidal and estuarine fish species.

Material and Methods

Field sites were chosen along sections of the Río Claro, Río Pavo, Quebrada Camaronal, Q. Danta, two small streams which emptied directly into the ocean, the headwaters of a small, unnamed stream, and one rocky intertidal pool. Additional fish collections and notes were made in intertidal regions of bedrock substrate (A), an oxbow lake near the mouth of the Río Sirena (B), the Río Sirena estuary, and sections of streams between the selected field sites. Maps were constructed for each field site containing: Profiles of stream depth, poll or riffle length, stream width, substrate composition, and the location of potential fish refugia (i.e., undercut stream bank, roots, logs, boulders, etc.). The length of each field site was delineated by the natural boundaries of the pool or riffle under investigation. Consequently, a pool field site in a river was often much longer than a pool in a smaller stream. Water current velocity was determined by tossing a 35 mm film canister, half-filled with water, into the region of greatest current and timing its passage rate over a designated distance. At each field site, the following data were recorded: 1) pH; 2) salinity (ppt); 3) temperature; 4) maximum water current velocity; 5) the abundance of each fish species present; and 6) the relative ratio of juveniles to adults of each fish species present. The presence of epiphytic algae, zooplankton, crustaceans, insolation, and fruiting trees was also noted at each site. Each field site was photographed to supplement the mapped information in later analyses.

Fishes were collected by dipnetting, seining, fish traps, angling, and by hand. Habitat utilization and estimates of the relative abundances of fishes were made by direct observation from above the water's surface and snorkelling below the water's surface during normal stream discharges. Special attempts were made to trap or dipnet rare or nocturnal fishes under sections of eroded stream bank. Selected fishes were measured for standard length and their stomach morphology and contents were examined. One to six specimens of each species collected were preserved in 10 percent formalin and later deposited in the Texas Natural History Collection of the Texas Memorial Museum, University of Texas, Austin.

Descriptions of Field Sites

Corcovado park is located on the extreme western edge of the Osa peninsula of Costa Rica's Pacific coast. The park is approximately 41,800 ha and lies at approximately 8°30′ N latitude and 83°30′ longitude. Corcovado Park contains extensive areas of primary tropical rainforest plus patches of regenerating second growth, including dense stands of *Heliconia, Calathea, Trema, Piper, Cecropia* and species of other plant genera (Janzen, 1979). The park received 4701 mm of rainfall in 1980 and averaged 364.4 mm over 1979, 1980, 1981 during the period in which the present study was conducted (June 25 to July 28). This period is in the early stage of the major annual rainy season of this region. The streams and rivers of the park flow over Cretaceous volcanic and sedimentary rocks and, to a lesser degree, Quaternary alluvial deposits (Janzen, 1979).

The location of each field site is provided in Figure 1. Fish species numbers, physical parameters of the water, and stream length, width, and maximum depth are provided in Table 1. The following are verbal descriptions of the general habitat conditions present at each field site.

Sites 1 and 3 are shallow, swampy pools at the headwaters of small streams which ultimately empty into the Río Sirena. The pools contained much emergent vegetation, including *Heliconia* sp. Rotting *Heliconia* leaves served as refugia for fishes and substrate for *Spyrogyra* sp. and other species of filamentous green algae. The bottoms of these pools were covered with thick layers of vegetative detritus and mud. At midday, direct sunlight was transmitted through the secondary growth forest, producing scattered patches of sunlit and shaded water in each pool. No observable water current was present at sites 1 and 3.

Sites 2, 4, 5, 7, 8, 9, and 11 are pools in the Quebradas Danta and Camaronal. All pools contained regions of gravel, sand, and leaf litter substrate. Epiphytic blue-green algae and diatoms were usually present on rocks in the shallow marginal areas or deeper regions containing observable current in these pools. Each pool is bordered at one side by an area of eroded (undercut) bank, usually with tree root structures or bedrock above. A small portion of most pools was exposed to direct sunlight during midday, and these were often associated with limited algal growth when suitable substrates were present.

Site 6 is located at the extreme headwaters of the Quebrada Camaronal. This was the last pool observed to contain fish (3 specimens of *Agonostomus monticola*) as one traveled this fork upstream. Stream gradients are much steeper and many moss—and lichen—covered boulders are present in this region of the stream. Leaf litter, bedrock, and gravel comprised the substrate, and very little observable algae was present at this site. The entire pool remained shaded by primary forest throughout the day.

Site 10 is a shallow riffle section of the Q. Camaronal with a coarse gravel, sand, and leaf litter substrate. Most of the riffle was exposed to direct sunlight at midday, and this appeared to support thin growths of epiphytic blue-green algae and diatoms.

Site 12 is located at the mouth of the Q. Camaronal where it empties into the Río Sirena estuary. Site 12 grades from a deep, narrow stream pool, bordered by bedrock, to a shallow slough flowing over rocks, coarse gravel, and finally sand and silt. The entire site is exposed to direct insolation through most of the day and supported diatoms on the rock surfaces.

Sites 13 and 14 are located in two separate small, shallow streams which flow through areas of extensive secondary forest growth adjacent to the coast. These streams empty directly into the ocean over sandy beach. The substrate of site 13 consisted of sand and the pool margins were composed primarily of grasses and sedges. Site 13 was exposed to insolation throughout most of the day, yet no significant algal growth was observable. Site 14 was entirely shaded and has a sand, soil, and leaf litter substrate. Clumps of emergent understory vegetation were scattered throughout site 14. These streams are probably ephemeral, with very restricted flow during the major dry season.

Sites 15 and 17 are large pools in the Río Claro which have bedrock and gravel substrates. Thin growths of blue-green algae and diatoms were present in the shallow marginal areas and swift headwaters and tailwaters of each pool. Leaf litter deposits were generally present among the rocks at the pool margins. Major portions of both pools were exposed to direct sunlight at midday.

Site 16 is a swift riffle area of the Río Claro. The substrate is comprised of coarse gravel and rocks. Most of this area is exposed to direct sunlight at midday, and a thin layer of algae is present on some rocks, particularly in shallower marginal regions of the riffle.

Site 18 is located in a channel formed by the presence of a sand bar near the edge of the Río Claro estuary. The substrate here is comprised of sand and fine silt deposits. The area is exposed to direct sunlight throughout the day, yet no significant epiphytic algal growth was detected. Forest litter was commonly deposited along the banks of the channel following floods and high tides.

Site 19 is a large pool of the Río Pavo approximately 50 m upstream from the crossing of the park's Casa Marenco trail. The substrate at this site was primarily fine gravel and sand. Unlike the pools of the Río Claro (sites 15 and 17) several fallen trees provided cover for the fishes. The entire pool was exposed to sunlight at midday, and very limited growths of epiphytic algae were present in the shallower regions.

Site 20 is an isolated intertidal pool at low tide, which has a sand and bedrock substrate. Numerous rocks were scattered throughout the pool, providing cover for many small marine fishes. The pool is exposed to direct sunlight throughout the day, and thin layers of epiphytic algae were present on many rocks. At high tide, site 20 is inundated by over 3 m of sea water and is exposed to constant wave action.

Observations

The number of species at each freshwater field site was extremely variable, ranging from one (sites 6, 13, 14) to 15 (site 19). In addition to providing total species numbers, Table 1 summarizes the number of primary division, secondary division, peripheral, and marine fish species at each site. No continuous pattern emerged as total species richness was tracked from the headwaters of each river and stream to its mouth. SPSS (Statistical Package for the Social Sciences, Nie *et al.*, 1975) was used to compute a multiple regression analysis of total numbers of fish species and stream current, maximum depth, maximum width, and the length of each field site. The results, summarized in Table 2, indicate that approximately half of the total variance is explained by differences in stream width. Additional variance within the pattern of species richness is explained by depth, current, and site length, in order; and together these four variables accounted for 73 percent of the variance. The ratio of the numbers of peripheral and marine species to the number of freshwater division species increased from 1.0 at the headwaters of the Q. Camaronal to 12.0

at its mouth. A simple regression of peripheral and marine to freshwater species for the seven sites on the Q. Camaronal resulted in a positive trend ($r^2 = .494$), however this was statistically nonsignificant ($F = 4.873$, $df = 1, 5$, $p = .078$). The distribution of freshwater, peripheral, and marine division fishes in the park does not correlate with salinity gradients since dissolved solids were uniformly low (< 1 ppt) throughout the streams and rivers (Table 1). The exceptions were the two river estuaries during high tides (Table 1).

The distribution and habitat affinities of each fish species within the park are presented in Table 3. *Astyanax fasciatus* was by far the most abundant and widely distributed primary freshwater fish species in the area. *Brachyrhaphis rhabdophora* was the most numerous secondary division species and was present at 14 of the 19 freshwater field sites. The distribution of *Poecilia sphenops* was much more restricted to regions of filamentous green algal growth. *Poeciliopsis turrubarensis* and *Oxyzygonectes dovii* were limited to the Río Sirena estuary and adjacent stream mouths where *B. rhabdophora* was absent.

Among peripheral fishes, *Awaous transandeanus, Sicydium pittieri, Gobiomorus maculatus, Eleotris picta,* and *Agonostomus monticola* were distributed far inland in significant numbers. *S. pittieri,* in particular, may reproduce in freshwaters as evidenced by the numerous juveniles throughout its distribution and the presence of a brilliantly colored territorial male in the middle reaches of the Q. Camaronal. Larger, predatory peripheral division and marine fishes (*Centropomus* and *Lutjanus* spp.) were present in significant numbers in the pools of rivers, even far inland (site 19). The abundance of these forms fell off sharply as one traveled toward the headwaters of the smaller streams and pool volumes declined. Juveniles of *Pomadasys bayanus* were commonly encountered in pools of the streams. Several individuals were observed to exhibit intraspecific aggression near regions of cover such as eroded stream bank. A single adult specimen (~ 1.5 m standard length) of the sawfish, *Pristis* sp., was observed at site 19 and one other location of the Río Pavo.

The most abundant fish species of the intertidal zones appeared to *Abudefduf analogus, Hypsoblennius striatus,* and *Bathygobius ramosus.* The assessment of the abundances of species such as *Gobiesox* sp., *Gymnothorax* sp., and *Malacoctenus zonifer* was hampered by the presence of many deep, undercut bedrock crevices utilized by these forms.

Preliminary information on the food habits of the principal freshwater-dwelling fishes of the park is presented in Table 4. Epiphytic algae and small shrimp of the family Palaemonidae apparently comprised the major autochthonous basis for the ichthyomass sustained in the rivers and streams. Major allochthonous sources of food input were forest vegetative detritus, mature fruits and seeds, and terrestrial insects, including ants. Aquatic snails were very abundant in the Río Claro, but only minor components of the Río Pavo and stream ecosystems. Other foods utilized were crayfish, aquatic insect larvae (Ephemeroptera), and microcrustaceans.

A striking characteristic of the streams at Corcovado is the paucity of autochthonous primary productivity, and the apparent extreme paucity of aquatic insects and zooplankton. Preliminary schemes for the trophic interactions of the communities of the Q. Camaronal (Fig. 2) and Río Claro (Fig. 3) were constructed based on the approximate relative abundances and food habits of each species. In both systems the major source of primary production takes the form of allochthonous input from the rainforest. Snails and shrimp comprised a much greater proportion of the "primary aquatic consumer" trophic level in the Río Claro than in the Q. Camaronal. Both communities are representative of a "food web" trophic structure, wherein many species populations utilize food resources from the same broad categories, or utilize food from two or more trophic levels. The species which comprised the lower trophic levels of the two systems were quite similar, however the Río Claro supported several more predatory species in the higher trophic levels (Figs. 2 and 3).

Although the food habits data for Corcovado fishes should be considered preliminary due to low sample sizes, several species exhibited fairly rigid selection for specific items. Fruits and seeds constituted the major portion of the diet of *A. fasciatus*, and to a slightly lesser degree *H. savagei*. Several species appeared to be strict algal grazers, including *P. sphenops* (green algae, esp. *Spyrogyra* spp.), *P. turrubarensis* (diatoms), and *S. pittieri* (diatoms and blue-green algae). The diets of *B. rhabdophora* and *A. monticola* consisted of terrestrial insects, with *B. rhabdophora* consuming mostly ants and tiny dipterans. The gut of the single analyzed specimen of *Sphoeroides annulatus* was packed with many aquatic snails and shell fragments. Several *Awaous transandeanus* were observed sucking up portions of fine gravel and sand substrate and allowing the inorganic particles to sift through their opercular openings. One adult *A. transandeanus* at site 16 was observed to periodically dash up from the substrate to capture individual particles of drifting detritus. The gut contents of two individuals revealed only fine particles of detritus.

Discussion

With the addition of *Oxyzygonectes dovii*, the present study increases the number of known freshwater division fishes at Corcovado (Constantz *et al.*, 1981) to seven. To the previous list of 14 fishes with marine affinities present in the park (Constantz *et al.*, 1981), this study reports 13 additional peripheral division and marine species, plus 10 additional marine species from intertidal zones. The three pipefish specimens, which were returned to the Texas Natural History Collection, were determined to be *Pseudophallus starksi*. *Pseudophallus elcaptanense* was reported as moderately abundant in the Q. Camaronal by Constantz *et al.* (1981), where two of my specimens were collected. *Gobiesox potanius* and *Rhamdia wagneri* were not observed during the study although both were previously reported as rare in the Q. Camaronal. Despite the fact that they were reported in slightly different manners, there appear to be major disparities in the approximations of the abundance and distribution of many of the fishes between 1979 (Constantz *et al.*, 1991) and 1982.

This may be due to differences in season, since the 1979 observations were made during the major dry season and the 1982 observations during the early portion of the major wet season. Differences in collecting techniques and censusing methods may have also contributed to differences in abundance estimates.

The ichthyofauna of the park's freshwater ecosystems is a mixture of freshwater, peripheral, and marine division forms. Certainly the composition of these communities is temporally dynamic in nature, and they will ultimately require detailed longitudinal studies before the factors influencing their structure are fully understood. If, as indicated by Table 2, stream volume has a major influence on species richness, then major differences in the number of peripheral and marine division fishes might be expected between wet and dry season censuses. Several investigations in a variety of temperate and tropical lotic systems have also supported the view that stream volume, width, and/or discharge may explain a major portion of the variability observed within fish species diversity patterns (Gorman and Karr, 1978; Smith, 1981; Livingstone *et al.,* 1982). I hypothesize that many more individuals of the marine division species join the ichthyofaunas of small coastal tropical streams, such as those at Corcovado, during wet seasons when stream volumes, discharge rates, and food resources are higher. Allochthonous food input to the Tortuguero estuary of eastern Costa Rica was found to be much higher during the wet seasons (Nordlie and Kelso, 1975). In a small Panamanian stream, fish foods were more abundant during the wet season (Zaret and Rand, 1971). During the dry seasons at Corcovado, many marine fishes may be excluded from freshwaters due to competition with freshwater and peripheral division fishes. In reviewing the distributional patterns of African freshwater fishes, Roberts (1976) noted that, when present, freshwater division fishes tend to exclude more euryhaline forms from inland habitats. Tiny palaemonid shrimp were extremely numerous in the streams and rivers of Corcovado during the early rainy season, and these should provide a major potential source of food for temporary marine invaders as well as permanent freshwater residents. The view, that primary and secondary division freshwater fishes dominate the ecosystems at Corcovado when stream volumes are lower, is also supported by the observation that freshwater division fishes comprised a greater proportion of the species richness as one traveled away from the mouths of streams.

Corcovado Park lies within the isthmian faunal province of Miller (1966) and Bussing (1976). This region of Central America is by far the richest in primary division freshwater fish species (Myers, 1966; Miller, 1966; Bussing, 1967), with most forms derived from South American faunal elements. Of the three primary division species present at Corcovado, *Astyanax fasciatus* and *Rhamdia wagneri* are reported to have limited tolerances to saline conditions (Miller, 1966; Bussing, 1976). Both of these species exhibit ubiquitous ranges in lower Central America, and *A. fasciatus* in particular extends from Argentina to southern Texas on the Atlantic slope (Miller, 1966). It is therefore quite likely that these species have utilized a coastal route for dispersal into this distal region of the Osa peninsula. If stream headwater captures had played a significant role in the dispersal of primary freshwater fishes into the park, more species would be expected. The degree of salinity tolerance by

Hyphessobrycon savagei is unknown. Like the primary freshwater fishes, the secondary division fishes of Corcovado are represented by several species which are ubiquitous in Central America. The presence of these seven primary and secondary division freshwater fishes suggests that these forms have dispersed into the Osa fairly recently (i.e., compared to major dispersals of these families along the mainland Central American slopes) and by way of coastal routes, possibly during periods of unusually high rainfall. The recent arrival of freshwater division fishes into the Corcovado region is further supported by Bussing's (1967) observation that a large number of indigenous species comprise the Costa Rican freshwater fish fauna. The peripheral and marine division fishes of Corcovado are primarily species which are widely distributed along the Pacific coast of Central America. Several species, such as *Agonostomus monticola, Centropomus undecimalis,* and *Mugil curema* are known from both coasts of Central America. Apparently, the presence of *Abudefduf analogus* in my collections represents the first report of this species for the Pacific coast of Central America.

The preliminary data on the diets of Corcovado fishes indicated that several freshwater and peripheral division species have fairly restricted feeding habits (Table 4). One marine invader, *Sphoeroides annulatus,* may specialize on snails, using its "beak–like" dentition to crush shells. Most of the marine species in freshwaters at Corcovado are large predators which apparently exploit the numerous shrimp and small fishes. Much more information is needed on the diets of these fishes before it can be determined if food resources are a limiting factor for marine fish biomass during the wet season. The descriptive information on stream habitat use by the fishes of Corcovado (Table 3) suggests that habitat selection could be one means by which fishes ecologically segregate during periods of depressed resources. This is an emerging generalization from recent studies of tropical stream (Zaret and Rand, 1971; Roberts, 1972; Bishop, 1973; Gorman and Karr, 1978) as well as temperate freshwater fish ecology (Winn, 1958; Allen, 1969; Mendelson, 1975; Symons, 1976; Werner *et al.,* 1977). The distributional patterns of fishes within the park (Table 3) probably relates most directly to habitat affinities. Consequently, the total species richness at each site should relate, not only to stream volume (Table 2), but also to environmental heterogeneity in terms of habitat diversity at each site. For example, *Poecilia sphenops* was only abundant in environments where there was low water current velocities and significant growth of filamentous green algae.

The freshwater ecosystems of Corcovado Park appear to be consistent with the physical characteristics of many tropical rainforest headwater streams (Myers, 1947; Roberts, 1972; Bishop, 1973; Lowe-McConnell, 1975). Their waters are apparently quite nutrient poor, contain little primary production, are often entirely shaded, exhibit low thermal variability, and receive seasonal patterns of rainfall. One major difference is the absence of high freshwater fish species diversity at Corcovado due to the peninsular effect. The Río Claro and Río Sirena also lack extensive stretches of lowland floodplains and extensive estuaries prior to their discharge into the Pacific Ocean. It is this unique combination of physical and biotic similarities and dissimilarities to other tropical regions which gives the freshwater ecosystems of Corcovado Park a tremendous potential for comparative tests of the factors governing the evolution of tropical stream fish communities. For example, I would predict that the large numers of palaemonid shrimp, supported largely by terrestrially-derived vegetative detritus, could support many more freshwater fishes in higher trophic levels during the rainy season, if they were introduced. The reproductive biology of the peripheral division fish species of the park remain virtually unknown. These fishes are very important components of many freshwater communities, and additional life history information could contribute much to clarifying the operational definitions of fish divisions based on marine dispersive abilities and ecology.

Acknowledgments

I would like to thank Frank Pezold for his extensive efforts in verifying and determining the identification of species collected at Corcovado Park. Clark Hubbs and Lawrence Gilbert provided important logistical assistance which otherwise would have made the study impossible. Thomas Grohman and Lawrence Gilbert aided in the collection of several fish species. Frank Pezold, Lawrence Gilbert, and John Rawlins provided important criticisms and suggestions during the preparation of the manuscript. I would especially like to thank the efforts of the Costa Rica National Park Service for their provision of a collecting permit and hospitality during the study. The data was compiled during participation in the U. T. Zoology 384L course in tropical ecology.

Resumen

Se investigaron las comunidades de peces de agua dulce en el Parque Nacional Corcovado del 25 junio al 28 de julio. Se observaron o recolectaron treinta especies de peces de agua dulce, así como diez especies que se encuentran solamente en zonas con influencia de las mareas.

Los peces de las divisiones de agua dulce más abundantes y extensamente distribuidos son *Astyanax fasciatus* y *Brachyrhaphis rhabdophora.* De los peces de la división periférica, *Sicydium pittieri, Awaous transandeanus, Gobiomorus maculatus* y *Eleotris picta* fueron los más extensamente distribuidos en las aguas dulces de la región. Varias especies de la división marina también se encontraron con frecuencia en agua dulce, entre otras, *Mugil curema, Pomadasys bayanus, Lutjanus colorado, L. novemfasciatus,* y *Spheroides annulatus.* Estas especies se encontraron en abundancia sobretodo en los ríos y las regiones bajas de los arroyos. El único ejemplar de pez sierra (*Pristis* sp.) observado, se encontró en el río Pavo casi a kilómetro y medio de la desembocadura.

Examinamos los contenidos de los estómagos de varios ejemplares de las especies dulceacuícolas más comunes. Los alimentos terrestres les eran muy importantes;

entre otros, pepitas, frutas, insectos (especialmente hormigas) y material orgánico. Ahora bien, la mayor parte de la comida autóctona en los regímenes de los peces fue algas, camarones y peces pequeños. La mayoría de los peces de las divisiones de agua dulce parecen tener hábitos de alimentación particulares.

La particularidad del hábitat en el arroyo de cada especie sugiere la posibilidad de que este factor pueda ser un método adicional de segregación ecológica.

Tomando en cuenta la información preliminar de que disponíamos sobre los hábitos de alimentación, se construyeron redes de alimentación para las comunidades de Quebrada Camaronal y río Claro. Se encontró que el ancho del arroyo se correlaciona positivamente con la riqueza de especies de peces. Con base en los estudios preliminares hechos en Costa Rica y Panamá, se ofrece la hipótesis de que los elementos marinos en las aguas dulces del parque bajan en número durante las estaciones secas. También que por lo menos cinco de los peces de las divisiones de agua dulce emigraron hacia el interior de la región por rutas costeras.

Literature Cited

Allen, K. R. 1969. Distinctive aspects of the ecology of stream fishes: A review. J. Fish. Res. Bd. Canada 26: 1429–1438.

Bishop, J. E. 1973. Limnology of a small Malayan river, Sungai Gombak, Monograph. Biol. 22. The Hague: W. Junk. 435 pp.

Bussing, W. A. 1967. New species and new records of Costa Rican freshwater fishes with a tentative list of species. Rev. Biol. Trop. 14: 205–249.

Bussing, W. A. 1976. Geographical distribution of the San Juan ichthyofauna of Central America with remarks on its origin and ecology. Pages 157–175 In T. B. Thorson, ed. Investigations of the ichthyofauna of Nicaraguan lakes. Lincoln: Univ. Nebraska.

Constantz, G. D., W. A. Bussing, and W. G. Saul. 1981. Freshwater fishes of Corcovado National Park, Costa Rica. Proc. Acad. Nat. Sci. Phila. 133: 15–19.

Gorman, O. T. and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.

Janzen, D. H. 1979. Use of Santa Rosa National Park and Corcovado National Park, Costa Rica, by biologists. Unpublished manuscript, Univ. Penn. 47 pp.

Livingstone, D. A., M. Rowland, and P. A. Bailey. 1982. On the size of African riverine fish faunas. Amer. Zool. 22: 361–369.

Lowe– McConnell, R. H. 1975. Fish communities in tropical freshwater. London: Longman. 337 pp.

Mendelson, J. 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. Ecol. Monogr. 45: 199–230.

Miller, R. R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966: 773–802.

Myers, G. S. 1938. Freshwater fishes and West Indian zoogeography. Smithson. Rpt. 1937: 339–364.

Myers, G. S. 1947. The Amazon and its fishes, Part 4. The fish in its environment. Aquar. J. 18: 8–19.

Myers, G. S. 1966. Derivation of the freshwater fish fauna of Central America. Copeia 1966: 766–773.

Nordlie, F. G. and D. P. Kelso. 1975. Trophic relationships in a tropical estuary. Rev. Biol. Trop. 23: 77–99.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical Package for the Social Sciences. New York: McGraw–Hill. 675 pp.

Roberts, T. R. 1972. Ecology of fishes in the Amazon and Congo basins. Bull. Mus. Comp. Zool., Harvard 143: 117–147.

Roberts, T. R. 1976. Geographic distribution of African freshwater fishes. Zool. J. Linn. Soc. 57: 249–319.

Smith, G. R. 1981. Effects of habitat size on species richness and adult body sizes of desert fishes. Pages 125–171 In R. J. Naiman and D. L. Soltz, eds. Fishes in North American deserts. New York: John Wiley & Sons.

Symons, P. E. K. 1976. Behavior and growth of juvenile Atlantic salmon *(Salmo salar)* and three competitors at two stream velocities. J. Fish. Res. Bd. Canada 33: 1766–1773.

Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Bd. Canada 34: 360–370.

Winn, H. E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces– Percidae). Ecol. Monogr. 28: 155–191.

Zaret, T. M. and A. S. Rand 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52: 336–342.

Table 1. The number of fish species and measures of stream physical parameters at each field site.

Site	Total No. species	1° FW.	2° FW.	Peripheral	Marine	Salinity (ppt)	pH	Temp.* (°C)	Current (m/s)	Max. depth (m)	Max. width (m)	Length of sample site (m)
1	4	1	2	1	0	< 1	6.5	27.0	–	.15	4.0	5.8
2	3	1	1	1	0	< 1	6.5	26.0	.11	.25	2.0	6.1
3	2	0	2	0	0	< 1	6.0	26.0	–	.28	5.2	9.1
4	7	2	1	4	0	< 1	7.0	25.2	.09	.90	5.7	14.6
5	9	1	2	5	1	< 1	–	25.2	.13	.64	9.2	15.2
6	1	0	0	1	0	< 1	7.0	24.5	–	.90	2.9	5.8
7	9	2	1	5	1	< 1	7.0	24.5	.10	.90	4.8	15.2
8	10	2	2	5	1	< 1	7.0	25.2	.05	1.10	7.7	15.2
9	10	2	1	5	2	< 1	7.0	25.5	.13	.70	6.6	12.7
10	3	0	1	2	0	< 1	7.0	25.5	.25	.23	3.3	9.1
11	11	2	1	6	2	< 1	7.0	24.5	.03	.60	5.3	26.5
12	13	0	1	5	8	< 1(L)**	–	24.5	.12	.61(L)	7.8(L)	52.0
13	1	0	1	0	0	< 1	6.5	25.5	.18	.30	2.1	5.0
14	1	0	1	0	0	< 1	6.5	24.8	.09	.12	5.0	12.4
15	14	1	1	5	7	< 1	7.0	25.0	.76	2.40	30.5	53.7
16	7	0	0	3	4	< 1	7.0	25.0	1.77	.40	11.6	30.5
17	15	1	1	6	7	< 1	7.0	25.0	.97	1.50	17.1	30.5
18	7+	0	0	2	5+	< 1(L) 5(H)	7.0	26.2(L)	.47(L)	1.00(L)	11.6(L)	16.8
19	15	2	1	7	5	< 1	7.0	–	[illegible]	1.20	35.0	100.0
20	4	0	0	0	4	19(L) 25(H)	7.5	29.0(L) 27.0(H)	[illegible]	.13(L)	7.6(L)	36.6
A	14	0	0	0	14	25(H)	7.5	27.0(H)	–		–	
B	2+	?	?	2+	?		–	–	–		–	
Sirena estuary	17+	0	2	3+	12+		–	27.0(H)	–		–	

* Temperature data was collected between 1000 and 1400 hr on various dates and merely reflect the relatively low variability of values between sites.

* (L) = low tide; (H) = high tide.

Table 2. Results of a stepwise multiple regression analysis of fish species numbers and measures of stream size.*

Step	Variable	Contribution to R^2	Partial F	Overall R^2	Overall F	Significance
1	Width	.519	18.340	.519	18.340	.001
2	Depth	.062	2.364	.581	11.088	.001
3	Current	.0001	.003	.581	6.933	.004
4	Length	.150	7.825	.731	9.521	.001

The regression equation is y (number of species) $= 1.780 + .420x_1$ (current) $6.320x_2$ (depth) $- .476x_3$ (width) $+ .228x_4$ (length).

Table 3. Locality, abundance, and habitat information for each fish species observed at the Sirena station of Corcovado National Park, June 25 to July 28, 1982.

Species	Localities	Relative* abun-dance	Ratio** adults/ juv's	Habitat affinities
Primary Division Fishes:				
Astyanax fasciatus	1,2,4,5,7,8,9,11,15,17, 19	A	100/0	Midwater; margins of rivers and deeper pools of streams in slow current
Hyphessorbrycon savagei	7,8,9,11,19	I	100/0	Surface-midwater; shallow areas of pools, esp. in headwater current
Secondary Division Fishes:				
Brachyrhaohis rhabdophora	1,2,3,4,5,8,9,10,11,13, 14,15,17,19	A	40/60	Usually surface; swamps and shallow marginal areas of pools, often in slow current
Poecilia sphenops = gilli	1,3,8	A	50/50	All depths; swamps and marginal areas of stream pools
Poeciliopsis turrubarensis	12, Sirena estuary	A	50/50	All depths; mouths of streams in current and at margins
Oxyzygonectes dovii	5, Sirena estuary	I	100/0	Surface; quiet regions of large pools in the lower reaches of streams and the Sirena estuary
Peripheral Division Fishes:				
Sicydium pittieri = altum	4,5,7,8,9,10,11,15,16, 17,19	A	40/60	Bottom; on rocks in current, esp. in stream riffles
Awaous transandeanus	2,4,5,7,8,9,10,11,12,15, 16,17,19	A	30/70	Bottom; on sand or gravel in current or at margins
Gobiomorus maculatus	1,4,5,7,8,9,11,15,17,19	A	40/60	Bottom, deeper pools of streams and margins of rivers
Eleotris picta	4,5,8,9,11,12,15,17,19, Sirena estuary	A	30/70	Bottom, often burried in leaf litter; deeper pools of streams and river margins; (nocturnal)
Agonostomus monticola	4,6,7,8,9,11,19	I	40/60	Midwater-bottom; deeper pools of streams in slow current
Centropomus undecimalis = nigrescens	5,11,12,15,17,18,19,B, Sirena estuary	I/A	10/90	All depths; larger pools of rivers and lower reaches of streams
Dormitator latifrons	B	A		All depths; in vegetation along lake shoreline
Bathygobius andrei	12,18, Sirena estuary	A		Bottom; over mud/silt substrate
Pseudophallus starksi	9,12,16,17,19	I	90/10	Bottom; in strong current or burried in leaves at margins of streams or rivers

Marine Division Fishes:

Mugil curema	12,15,17,18,19,20,A, Sirena estuary	A	40/60	Bottom; river margins, estuaries, and intertidal regions at various current velocities
Pomadasys bayanus	7,8,9,11,15,16,17,19, Sirena estuary		70/30	Midwater-bottom; deeper stream pools, esp. near undercut bank; juveniles in shallow fast current in rivers; adults in deep pools of rivers
Sphoeroides annulatus	12,15,17,18,A, Sirena estuary		100/0	Bottom; rivers in current or at pool margins; intertidal regions
Lutjanus colorado	12,15,16,17,18,19, Sirena estuary		60/40	Midwater-bottom; large river pools in current
Lutjanus novemfasciatus	12,15,16,17,18,19,A, Sirena estuary	A	60/40	Midwater-bottom; large river pools in current
Lutjanus argentiventris	11,12,15,16,17,19, Sirena estuary		10/90	Midwater-bottom; near steep or undercut rock banks
Eucinostomus sp.	5,15,17, Sirena estuary	I	0/100	Midwater; larger pools in lower reaches of streams; at margins of rivers
Pristis sp.	19	R	100/0	Bottom; larger pools of Río Pavo
Bathygobius ramosus	20,A	A	50/50	Bottom; over rock substrate in intertidal regions
Erotelis armiger	12, Sirena estuary	I	–	Bottom; over mud/silt substrate
Enypnias seminudus	A	–	–	Bottom; over rock substrate
Pseudojillus notospilus	A	–	–	Bottom; over rock substrate
Gobiesox sp.	A	–	–	Cling to rock surfaces
Malacoctenus zonifer	A	–	–	Bottom; over rock substrate
Hypsoblennius striatus	20,A	A	80/20	Bottom; over rock substrate
(Pleuronectidae) 1 sp.	12,A	R	–	Bottom; over mud or rock in slow current
Carcharhinus leucas	Sirena estuary	I	–	Generally occurs in estuary at high tide only
Caranx sp.	Sirena estuary	A	–	Generally occurs in estuary at high tide only
(Scombridae) 1 sp.	Sirena estuary	A	–	Generally occurs in estuary at high tide only
(Dasyatidae) 1 sp.	Sirena estuary	R	–	Generally occurs in estuary at high tide only
Gobionellus sagittula	12,18	A	10/90	Bottom; over mud/silt substrate
Abudefduf analogus	20,A	A	100/0	Midwater-bottom; rocky intertidal regions
(Serranidae) 1 sp.	A	R	0/100	Midwater-bottom; rocky intertidal regions
Gymnothorax sp.	A	–	0/100	Bottom; within rock crevices and under large rocks
Microdesmus sp.				Bottom; within algal mats and rock crevices

* A = abundant (generally 10 to 100+ individuals/field site), I = intermediate (generally 1 to 10 indiv./field site), R = rare (two indiv. or less observed in the park during the study).

** Approximations based on visual censuses.

Table 4. Results of the stomach contents analyses for the principal fish species inhabiting the freshwaters of Corcovado National Park.

Species	Stomach contents	Alimentary canal	No.	Standard length (mm)
Astyanax fasciatus	Fruits, seeds, insects	Short, sac-like	13	38-95
Hyphessobrycon savagei	Small seeds, ants	Short, sac-like	7	35-43
Poecilia sphenops = gilli	Green algae (esp. *Spyrogyra* spp.)	Long, coiled	3	58-90
Brachyrhaphis rhabdophora	Ants, small insects	Short, sac-like	7	18-46
Poeciliopsis turrubarensis	Epiphytic algae	Long, coiled	3	20-28
Oxyzygonectes dovii	Ants, small insects, epiphytic algae, detritus	Short, sac-like	2	48-80
Sicydium pittieri = altum	Epiphytic algae	Long, coiled	2	56-71
Awaous transandeanus	Detritus	Long, coiled	2	74-85
Gobiomorus maculatus	Small fish, shrimp, Ephemeroptera nymphs	Short, sac-like	5	45-158
Eleotris picta	Larval fish, shrimp, crayfish, snails, seeds, fruits, detritus, insects	Short, sac-like	7	38-200
Agonostomus monticola	Insects	Short, sac-like	2	81-123
Mugil curema	Detritus, algae	Long, coiled	3	25-88
Pomadasys bayanus	Shrimp, crayfish	Short, sac-like	4	133-188
nigrescens *Centropomus undecimalis*	Fish, shrimp(Ñ)	Short, sac-like	7	50-85
Sphoeroides annulatus	Snails	Sac-like, long, coiled	1	130
Lutianus colorado	Shrimp, fish(?)	Short, sac-like	3	132-165
Lutianus novemfasciatus	Fish, shrimp(?)	Short, sac-like	2	132-150
Lutianus argentiventris	Shrimp, fish(?)	Short, sac-like	2	66-140
Pseudophallus starksi	Microcrustaceans(?)	Short, sac-like	2	92-110
Eucinostomus sp.	Microcrustaceans(?)	?	1	12
Bathygobius andrei	Shrimp	Short, sac-like	2	15-63

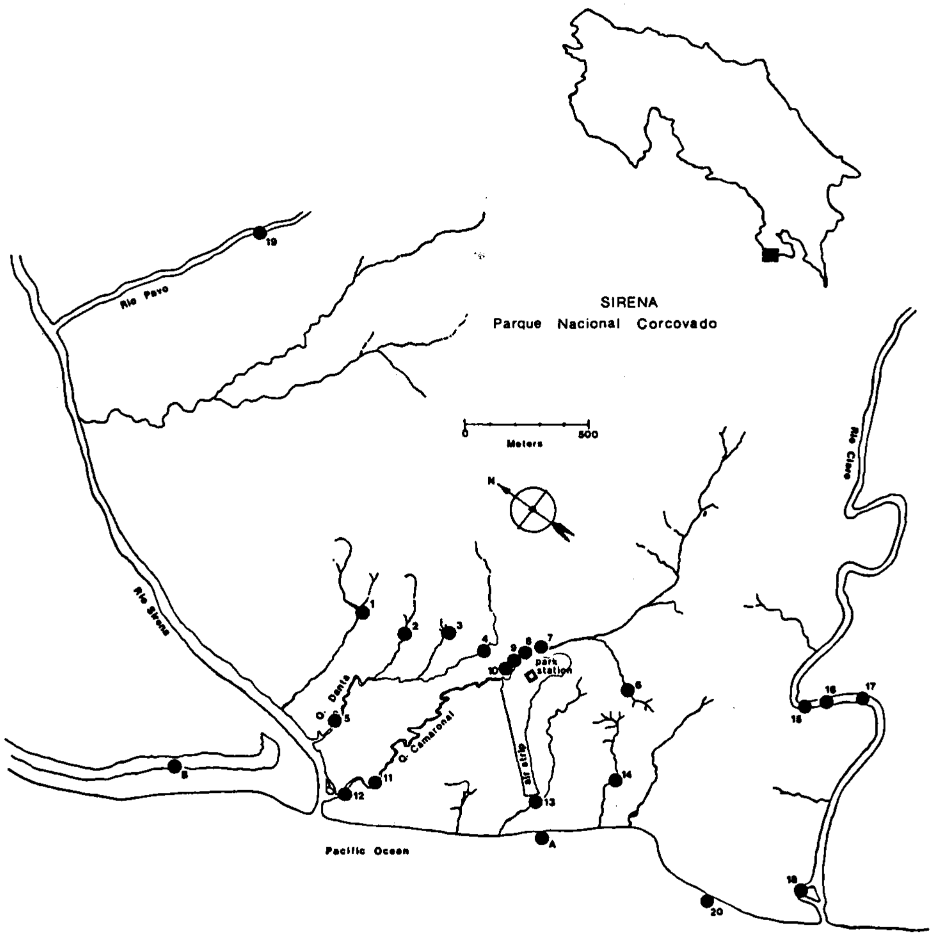

Fig. 1. Map of the area surrounding the Sirena station of Corcovado Park, Costa Rica and the locations of field sites.

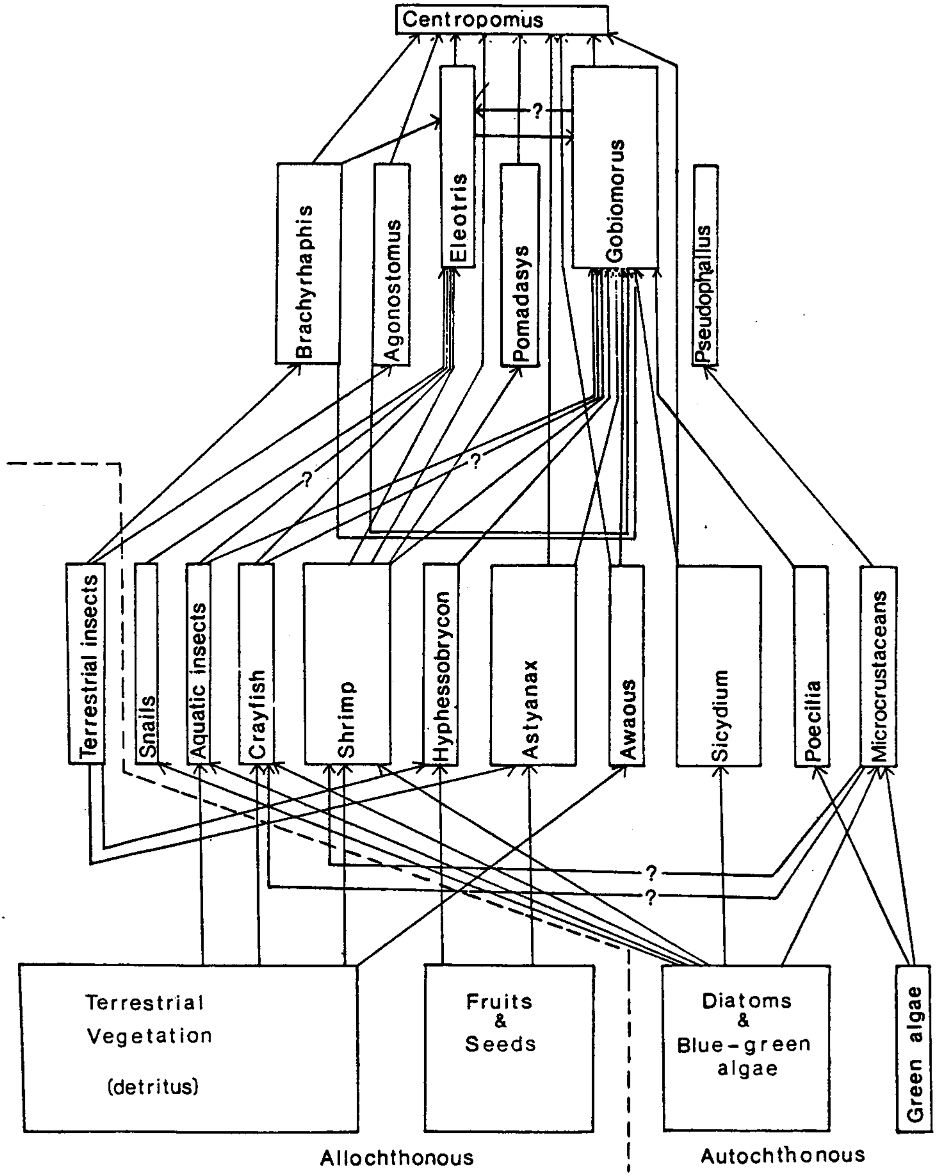

Fig. 2. Block diagram representing the trophic relationships within a typical community of the Quebrada Camaronal. The sizes of the blocks represent the approximate relative abundances of each component in terms of biomass, based on visual censuses.

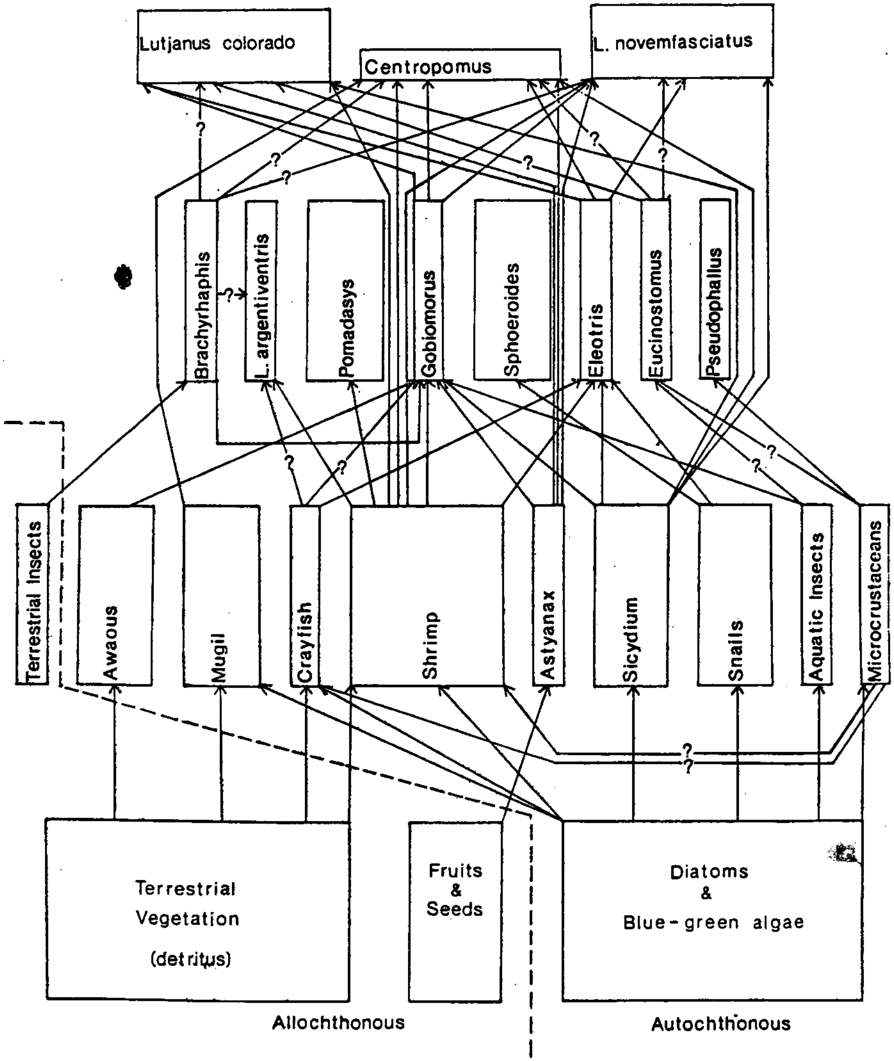

Fig. 3. Block diagram representing the trophic relationships within a typical community of the Río Claro.